

The generic status and affinities of *Paratilapia thomasi* Blgr 1915 (Teleostei, Cichlidae)

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Introduction and synopsis

When originally described (Boulenger, 1915), the species *thomasi* was placed in the genus *Paratilapia* Bleeker, 1868, then a large, catch-all assemblage of African Cichlidae. The artificiality of *Paratilapia* (*sensu* Boulenger) was recognized by Regan in his classical series of papers on the generic classification of African cichlid fishes, the first explicitly 'natural' classification of the group attempted (Regan, 1920: 34).

Regan (1922: 252) considered *Paratilapia thomasi* to be a member of the genus *Pelmatochromis* Steindachner, 1894. Regan's definition of that genus was based largely on osteological and dental features, most of which were present in *P. thomasi*, but some of which could not be checked because no skeletal material was available, as for example, the nature of the apophysis on the third vertebra, and the number of vertebrae.

That Regan's concept of *Pelmatochromis* embraced a polyphyletic taxon was recognized by Thys van den Audenaerde (1968:373), who in revising it, took into account features of soft anatomy as well as osteological characters, and certain ethological and other biological features such as coloration. *Pelmatochromis thomasi*, however, proved to be something of a stumbling block since neither alone nor in combination did its various characters qualify it for inclusion in any of the informal divisions into which Thys van den Audenaerde split Regan's *Pelmatochromis*. According to Thys van den Audenaerde (1968: 382), *P. thomasi* shows greatest affinity with *Hemichromis bimaculatus*. He did not, however, transfer the species to that genus, and nomenclaturally at least it remained in *Pelmatochromis*, even after Trewavas (1973) formally redefined that genus and excluded *thomasi* from it (Trewavas, *op cit.*: 14).

Most recently, Wilson & Loiselle (1980) placed *P. thomasi* in the genus *Hemichromis*. Their reasons for so doing are that, as a result of Loiselle's (1978) revision of *Hemichromis*, *P. thomasi* could not be excluded on the basis of its dentition, and that its breeding biology and live coloration also argued '... cogently for regarding this species as a specialized dwarf *Hemichromis*'.

Regrettably, I overlooked Wilson & Loiselle's paper when preparing my account on the anatomy and phyletic relationships of *Hemichromis* (Greenwood, 1985) and so did not discuss their arguments when considering the possible relationships of the taxon. I cannot, however, support their reasons for considering *P. thomasi* as a species of *Hemichromis*, particularly since it does not share with *Hemichromis* the unique and highly derived ethmopalatine articulatory system found in all members of that genus. Instead, *P. thomasi* has the plesiomorphic double type of ethmopalatine articulation found in most African cichlids and many other percomorph groups as well (see Greenwood, 1985: 139). Furthermore, although there are some undoubted and close similarities in the ethology and coloration of the two taxa, it is impossible to assess the significance of these features in a phylogenetic context (see p. 270 below). Finally, in addition to the ethmopalatine articulation, there are several other derived features in *Hemichromis* which are not shared with *P. thomasi* (see Greenwood, 1985).

That said, however, *P. thomasi* and the *Hemichromis* species do share, and apparently share uniquely, one very unusual feature. That is, the absence of a passage through the anguloarticular bone for the mandibular-preopercular laterosensory canal (Greenwood, 1985: 150). This feature, of course, was not known to Wilson & Loiselle (1980), or to Thys van den Audenaerde (1968) or Trewavas (1973). As far as I can tell from a wide-ranging examination of African, South American and Asian cichlids, combined with a survey of the literature and an examination of many other teleost taxa, the absence of a laterosensory passage through the anguloarticular is probably a feature shared only by *Hemichromis* and *P. thomasi*.

Thus, although it is a 'loss character', its very restricted distribution (a few species within a single family) would seem to strengthen the probability of it indicating a close relationship between those species possessing it. In other words, I would moderate the opinions I expressed recently (Greenwood, 1985: 168) and would now definitely suggest that *P. thomasi* and *Hemichromis* are recognised as sister groups.

If this sister-group status be accepted, the problem of formally ranking the taxa still remains. It might be argued that the relationship of *Hemichromis* to *P. thomasi* could best be indicated by ranking *P. thomasi* as a subgenus of *Hemichromis*. Against such a decision can be ranged the several autapomorphic features of *Hemichromis* (see Greenwood, 1985), in particular its unique and highly derived ethmopalatine articulation, and the absence of all but one synapomorphy shared uniquely by members of the two sister groups. For those reasons I consider the relationship would better be indicated if *P. thomasi* is ranked as a distinct genus, and that a suprageneric group comprising it and *Hemichromis* be recognised informally. The possibility that *Hemichromis* itself may comprise two very closely related lineages (*ie* subgenera) is discussed in Greenwood (1985: 168).

Study material

The study material listed in Greenwood (1985) provided relevant background information. In addition, the following material was examined:

All preserved specimens of *Pelmatochromis thomasi* currently in the collections of the BMNH. From that material two alizarin-alcian blue transparencies were prepared (*ex* 1981.6.19:10, 105–117, 44 mm & 50 mm SL) as were two dry skeletons (*ex* 1981.6.19: 105–117, *ca* 45 mm SL, and 1981.6.19:119–121, 50 mm SL). The gill-arch and jaw musculature were dissected in a 50 mm SL specimen *ex* 1981.6.19:119–121.

Radiographs were made from the three syntypes (1914.12.9:9–11), and from lots 1915.4.13:42–43; 1971.8.13:1; 1971.8.13:17, 1981.6.19:105–124; 1981.8.17:26–41, and 1982.2.4:1–10.

One specimen, *ca* 18 mm SL, of *Hemichromis* cf *H. bimaculatus* (1984.12.17:1, from Lamborini, Gabon, collected by R. Knowles) was partly dissected and stained with alizarin. One specimen of *Tilapia joko* (1982.11.9:24) was partially dissected.

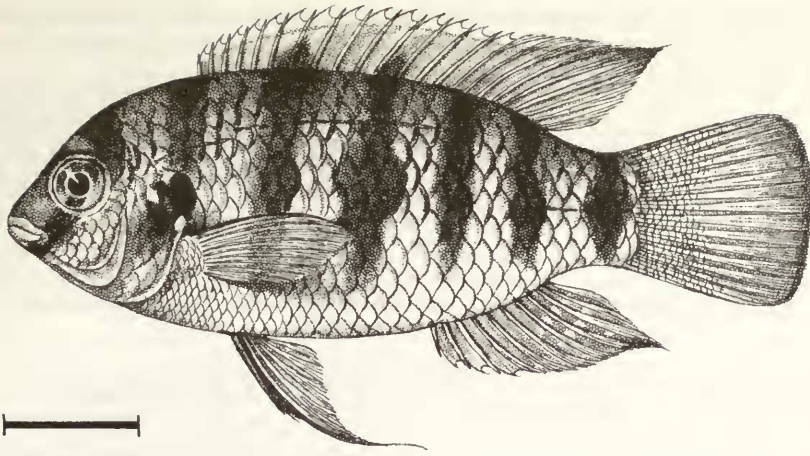


Fig. 1 *Anomalochromis thomasi*. Lectotype. 1.5 times natural size; from Boulenger, 1916.

ANOMALOCHROMIS gen. nov.
(Fig. 1)

SYNONYMY

Paratilapia (part): Boulenger (1915) *Ann. Mag. nat. Hist.* (8) 15: 202–204; *idem.* (1916) *Cat. Afr. Fw. Fish* 4: 331, fig. 192.

Pelmatochromis (part): Regan (1922) *Ann. Mag. nat. Hist.* (9) 10: 252.

Hemichromis (part): Wilson & Loisel (1980) *Cichlid Index* 4 (5): 1–2, in *Buntbarsche Bulletin* (*J. Amer. Cichlid Assn.* no. 78).

TYPE SPECIES. *Paratilapia thomasi* Blgr (1915). The original description, based on 3 syntypes only, is repeated unchanged in Boulenger (1916: 331), despite 3 additional specimens being listed there; this account is accompanied, for the first time, by a figure. On the basis of that figure, one syntype, 49.5 mm standard length (BMNH 1914.12.9:9) is now chosen as the lectotype.

ETYMOLOGY. The prefix is derived from the Greek *anomalous*, irregular, and refers to the unusual condition of the preopercular-mandibular lateral-line canal; the suffix *chromis* is a word now frequently used, in combination, for various genera of African cichlids.

DIAGNOSIS. Cichlid fishes with the articular surface of the neurocranial apophysis for the upper pharyngeal bones formed from the parasphenoid only. Vertebral column (excluding the fused PU_1 and U_1 centra) with 23–25 (mode 24) vertebrae; the apophysis for the insertion of *retractor arcuum branchialium* muscles situated on the 3rd vertebrae, its two halves not united ventrally. Palatine bone articulating with the lateral ethmoid in two places and not supported antero-ventrally by a lateral, peg-like process of the vomer. The anguloarticular bone lacks a canal for the passage of the mandibulo-preopercular lateral-line canal. Microbranchiospines present on the outer face of gill arches 2–4; 1 or 2 epibranchial gill-rakers on the first gill-arch, 5 or 6 on the ceratobranchial of that arch, and 1 at its epi-ceratobranchial articulation. Buccal tissue immediately anterior to the upper pharyngeal bones neither developed into a prominent pre-pharyngeal pad nor produced into a visor-like hanging pad. *Adductor arcus palatini* muscle with an insertion on the palatine. Scales on the body weakly ctenoid, their circuli arranged in an essentially 'gothic arch' pattern (clearly not of the 'Norman arch' type: see Trewavas, 1973:14, fig. 10); last scale of the upper lateral-line series not reaching a vertical drawn through the first scale of the lower series, there being a horizontal distance of about 2 scales between the two lines at this point; upper lateral-line, over most of its extent, separated from the base of the dorsal fin by one large

and one small scale. Pelvic fins in adult males with the first and second branched rays produced and filamentous, of equal length, and extending to the middle of the anal fin base.

DISTRIBUTION. The single known species, *A. thomasi*, is restricted to coastal rivers in Guinea, Sierra Leone and Liberia. In the original description of the species, its type locality is recorded as Matca, Sierra Leone, but in Boulenger (1916) it is given as Maka. No 'Maka' is listed in any of the gazetteers consulted, but there are at least 11 places named Moka and whose coordinates range from 7°08'N, 11°24'W, to 8°25'N, 12°02'W.

Notes on the osteology and anatomy of *Anomalochromis thomasi*

Osteology

Neurocranium (Fig. 2). In its general outline and proportions the neurocranium is somewhat foreshortened and deep; the supraoccipital crest is high.

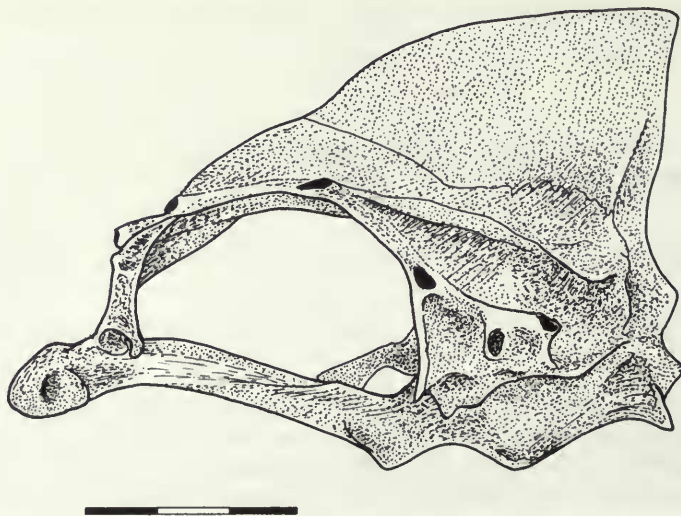


Fig. 2 *Anomalochromis thomasi*. Neurocranium in left lateral view. In this and following figures, the scale bars are in mm divisions.

The articular surface for the upper pharyngeal bones is formed entirely from the parasphenoid (*ie* of the *Tilapia*-type; Greenwood, 1978), and is carried on a low apophyseal eminence contributed to by the prootic and basioccipital of each side. The hind opening to the posterior myodome is relatively large.

The *lateral commissure* is narrow and strut-like, and there is no internal jugular bridge anterior to it. There is, however, a well-developed and prominent, dorsally directed spur from the prootic between the foramina for the 3rd and the 5th cranial nerves. This spur does not contact the upper part of the prootic, neither is it connected with that region of the bone by a ligament.

The *ethmoverine* region of the skull is relatively short, and lacks the casket-like elevation of the vomer which is so characteristic of this region in *Hemichromis* (*cf* fig. 1 in Greenwood, 1985 with Fig. 2). Judging from the condition found in two alizarin transparencies (in which the neurocranium is *ca* 11–12 mm long), the supraethmoid does not contact the vomer and, in consequence, a large area of the ethmoid cartilage is exposed. The anterior margin of the supraethmoid does, however, extend forward to a point where it is level with the anterior margin of each lateral

ethmoid's medial arm. The situation in both these specimens of *A. thomasi* very closely resembles that illustrated by Trewavas (1973: 22, fig. 4) for *Sarotherodon shiranus*. The length of the *S. shiranus* skull is not given, but judging from the scale of the figure it is about 5 or 6 times longer than the *A. thomasi* skull examined.

In adult specimens of those *Hemichromis* species I have studied the vomer and supraethmoid are in close contact laterally, and are separated medially only by a small rostral fenestra (Greenwood, 1985). Recently I was able to study the neurocranium in a small *Hemichromis* cf. *H. bimaculatus* of about 19 mm standard length. Here, although the vomer is produced dorsally into its typical casket-like medial crest (see above; also Greenwood, 1985) it differs from the adult condition because it is not in contact with the supraethmoid. Indeed, the two bones are widely separated and an expansive area of the ethmoid cartilage is visible, a situation contrasting markedly with that seen in specimens of 70 mm standard length.

Clearly, at least in this species of *Hemichromis*, there are marked ontogenetic changes in the spatial relationships of those bones contributing to the ethmoverine skull region. When the adult condition of *A. thomasi* is compared with the juvenile and adult conditions in *Hemichromis*, it would seem to be interpretable as a paedomorphic one. Wilson & Loiselle (1980) give the maximum adult sizes for male and female *A. thomasi* as, respectively, 80 and 70 mm standard length; no fishes of that length were available to me, so it was impossible to investigate the condition of the ethmovomerine complex in *A. thomasi* specimens in the upper part of that species' size range.

All specimens of the various *Chromidotilapia* and *Pelvicachromis* species examined (all, it should be noted, larger than the *A. thomasi* available) have the vomer and supraethmoid in contact, but, *pace* Trewavas (1973: 22), in *Pelmatochromis buettikoferi*, type species of that genus, the bones do not contact one another. The possible phyletic significance of these differences is currently under review (see also discussion in Trewavas, 1973).

Anomalochromis thomasi has a shallow *hyomandibulad shell*, a depression in the ventrolateral aspect of the neurocranium associated with the origin of the *levator externi* muscles of the gill arches (see Barel *et al.*, 1976). In *Hemichromis* the shell is a deep, dorsally directed and pit-like indentation. In *A. thomasi* the lateral awning is much shallower than that of *Hemichromis*, and, like the *hyomandibulad shell*, conforms to the modal cichlid type (Greenwood, 1985: 142).

There are no outstanding peculiarities in the morphology of the dorsicranium, nor are there any noteworthy characteristics associated with the otic region.

Gill-arch skeleton and the lower pharyngeal bone. Unlike *Hemichromis* (see Greenwood, 1985: 150–153) the gill-arch skeleton of *A. thomasi* is, in general, of the supposedly generalized type found in such haplochromine species as *Astatotilapia elegans* (see Barel *et al.*, 1976; Stiassny, 1981 & 1982).

The *epibranchials* of all four arches are relatively less elongate than those in *Hemichromis*, and epibranchial I has a long uncinat process, about three times the length of its process for articulation with the first pharyngobranchial; the angle between the uncinat and pharyngobranchial processes is small, about 10°, and the former process is directed posteriorly. As in most cichlids, no interarcual cartilage is developed.

Epibranchial II has a large, anvil-shaped cartilage associated with its anterior border. The cartilage is much larger than its counterpart in *Hemichromis*, and is comparable with that of *Pelmatochromis nigrofasciatus* figured by Trewavas (1973; fig. 11). A well-developed cartilage on this epibranchial is apparently the modal condition for cichlids (Stiassny, 1982; Greenwood, 1985: 151).

Epibranchial IV has a prominent and well-developed shank spine, and an expansive but not elongate quadrangular area. In both these features *A. thomasi* shows the generalized cichlid condition and thus differs from *Hemichromis* (Greenwood, 1985: 151; fig. 15).

The pharyngobranchial elements also conform to the generalized cichlid condition, and pharyngobranchial III is noticeably less rectangular in outline than is its counterpart in *Hemichromis*. A prominent 'frayed zone' (Stiassny, 1981) is present on the posterior border of the 4th upper pharyngeal tooth-plate.

The *ventral part* of the gill-arch skeleton, like that in *Hemichromis*, shows no peculiar or unusual features (Greenwood, 1985: 153).

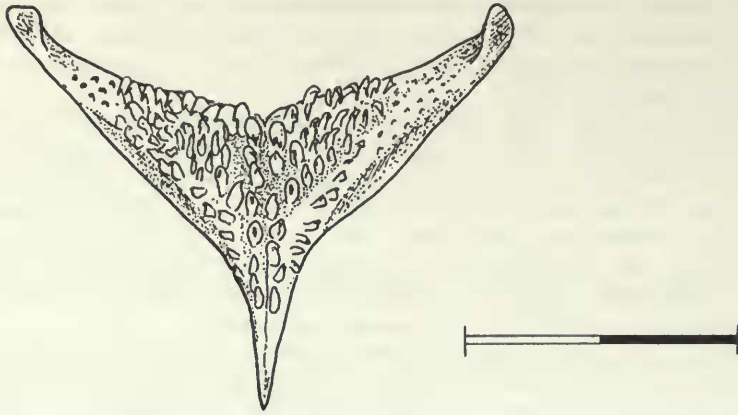


Fig. 3 *Anomalochromis thomasi*. Lower pharyngeal bone, occlusal view.

Microbranchiospines are present on the outer face of the 2nd to 4th ceratobranchials, and although small are quite obvious and consistently present.

The lower pharyngeal bone is illustrated in Fig. 3. Its short and broad outline resembles that in *Hemichromis* species; in *Pelvicachromis* and *Chromidotilapia* the bone has a more elongate and arrowhead-shaped outline, whilst the outline of the bone in *Pelmatochromis* is intermediate between the *Hemichromis* and *Pelvicachromis-Chromidotilapia* types.

Palatoquadrate arch and suspensorium (Figs 4a & B). There are few outstanding features in this region of the orobranchial skeleton which, in most respects, is of the plesiomorphic pattern found in many African cichlids. The *palatine bone* has a double articulation with the ethmoid region; that is: anteriorly with the lateral face of the lateral ethmoid near that bone's junction with the vomer, and posteriorly, with a low but distinct 'drum facet' on the ventro-medial face of the lateral ethmoid. In this feature *A. thomasi* differs markedly from *Hemichromis* where the articulation is a single and specialized one confined to the anterior face of the lateral ethmoid (see discussion in Greenwood, 1985: 139). Parenthetically it can be noted that in the small *Hemichromis* (19 mm SL) mentioned on page 261, the ethmopalatine articulation is exactly like that in the largest *Hemichromis* examined.

The palatine in *A. thomasi* also differs from that bone in *Hemichromis* since it has a distinct ridge developed on its lateral face, a plesiomorphic feature seemingly uncommon amongst African cichlids (Cichocki, 1976: 82 & 150; Oliver, 1984: 16).

The palatine and entopterygoid in *A. thomasi* are in contact ventrally, but dorsally their margins diverge very slightly (Fig. 4).

Together, the *hyomandibula* and *metapterygoid* bones contribute to the formation of a large *calyx*, with the metapterygoid also providing the incomplete anteroventral wall of this structure. It is thought that the calyx is a plesiomorphic feature; it is not developed in *Hemichromis* (Greenwood, 1985: 145-146).

The hyomandibular flange is relatively broad (Fig. 4) and does not contact the metapterygoid anteriorly, thus leaving a distinct anteromedial gap between the two bones. The shank of the hyomandibula is slender, its length contributing to slightly less than a third of the bone's entire length.

The *symplectic* has an unusual and somewhat sigmoidal shape (*cf* Fig. 4 with fig. 6 in Greenwood, 1985), with a noticeable gap between the ventral margin of its middle section and the rim of the preoperculum.

Hyoid arch (Fig. 5). The branchiostegal rays are fine and elongate; the greater part of each ray is cartilaginous and only its proximal quarter to third is strongly ossified. A large cartilaginous area is interposed between the ossified portions of the epi- and ceratohyal elements.

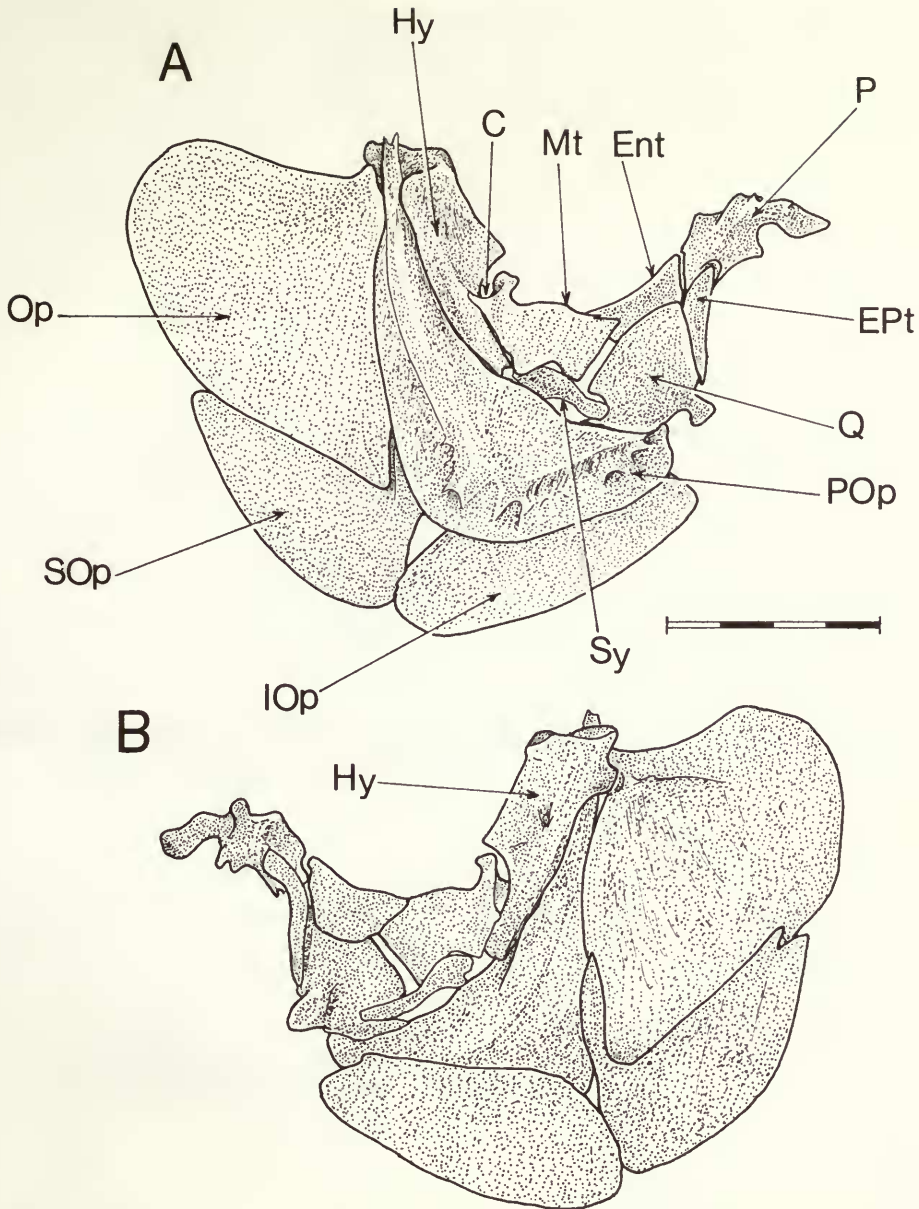


Fig. 4 *Anomalochromis thomasi*. Right palatoquadrate arch and opercular series: A, lateral view; B, medial view. C = Calyx. Ent = Entopterygoid. EPT = Ectopterygoid. Hy = Hyomandibula. IOp = Interoperculum. Mt = Metapterygoid. Op = Operculum. P = Palatine. POp = Preoperculum. Q = Quadrate. SOP = Suboperculum. Sy = Symplectic.

Jaws. The *maxilla* (Figs 6B & C) is rather foreshortened, slightly curved, and has its ventral margin incurved posteriorly where it is drawn-out into a distinct point. The mediad curvature of the bone's shank between the premaxillary saddle and the shank-ridge is much less obvious than the curvature in some *Hemichromis* species (eg *H. fasciatus* and *H. bimaculatus*) but is about equal to the curvature in *H. letourneuxi*. The outward inclination of the shank-ridge in *A. thomasi* is less pronounced than in any of the *Hemichromis* species examined (Greenwood, 1985: 148; fig. 12).

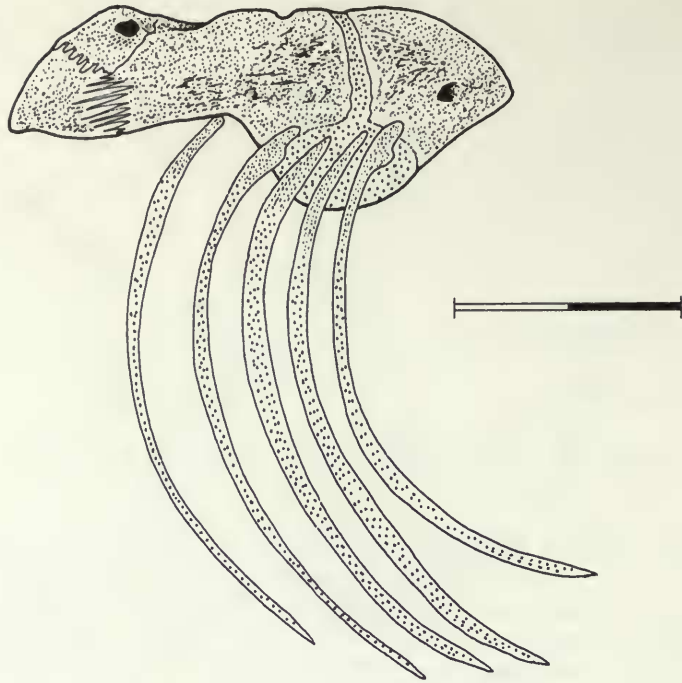


Fig. 5 *Anomalochromis thomasi*. Hyoid arch, left side, in lateral view. Stippled areas are cartilaginous or very poorly ossified.

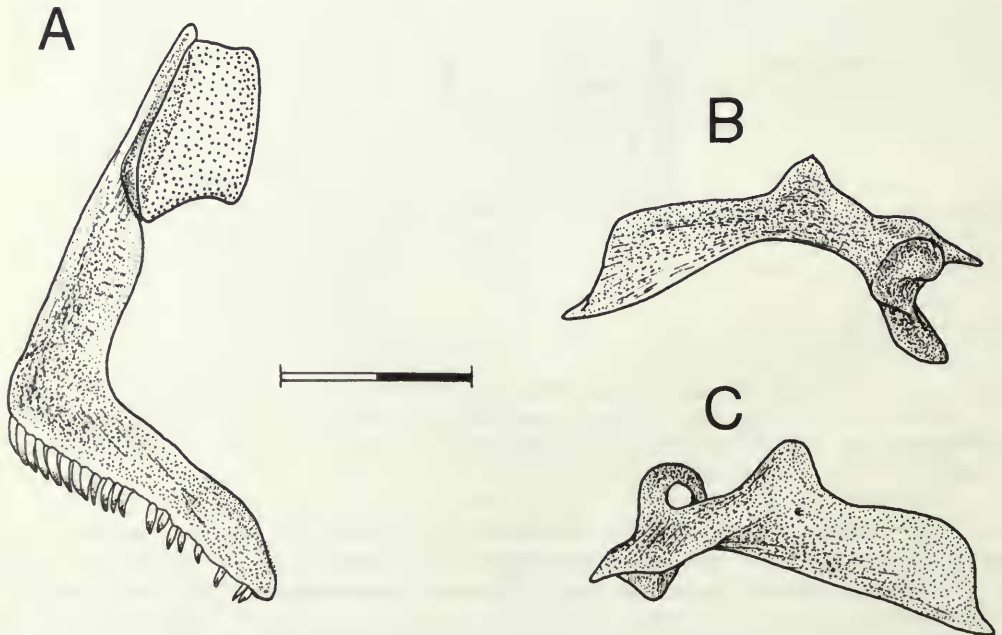


Fig. 6 *Anomalochromis thomasi*. A, Left premaxilla, in lateral view; the rostral cartilage is stippled; B & C, left maxilla in, respectively, dorsal and lateral views.

The ascending process of the *premaxilla* (as measured from its distal tip to the level where the process becomes indistinguishable from the dentigerous arm) is but slightly shorter than the dentigerous arm; the articular process extends distally to a point slightly more than half way along the ascending process. The dentigerous arm has almost no ventral curvature to its posterior tip, and the alveolar surface reaches nearly to the posterior limit of the arm.

There is a large, very thick and cushion-like *rostral cartilage*, which is oval in cross-section and is tightly applied to the ascending processes of the premaxilla (Fig. 6A).

The *dentary* (Fig. 7) has a very low coronoid process, and is a generally foreshortened and deep bone with four lateral-line sensory canal openings. Teeth in the outer series of the bone extend onto the anterior margin of the coronoid process as far as its crown.

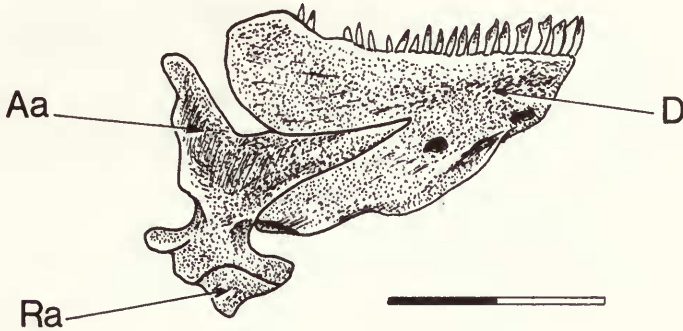


Fig. 7 *Anomalochromis thomasi*. Right mandible; viewed from a very slightly ventro-lateral aspect. Aa = Anguloarticular. D = Dentary. Ra = Retroarticular.

The *anguloarticular* (Fig. 7) is noteworthy for the complete absence of any tube, fossa or foramen for the passage of the preopercular sensory canal into the dentary. Such a condition is one apparently shared only with *Hemichromis* amongst the cichlids; if it also occurs amongst other teleosts it is of very rare occurrence and has not been recorded (see discussion, p. 258).

Infraorbital bones (Fig. 8). Apart from the relatively stout and well-ossified lachrymal (1st infraorbital) the bones in this series are very poorly ossified and delicate. For that reason, and because the available specimens were not suitably preserved for finer osteological study, it has proved difficult to give a precise account of this series.

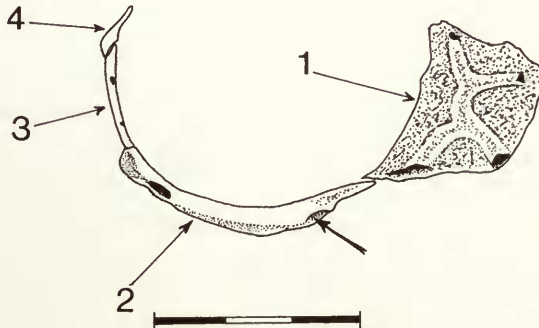


Fig. 8 *Anomalochromis thomasi*. Right infraorbital series. 1-4: First (lachrymal) to fourth infraorbital bones. Arrow indicates anterior opening of second bone.

The 1st infraorbital (lachrymal) has four laterosensory canal pores, the presumed plesiomorph condition in African cichlids (Greenwood, 1985: 165). The posterior pore lies at some distance from the anterior opening in the second bone of the series; the mouth of that opening lies in the same horizontal as the posterior pore in the lachrymal but is directed ventrally and not horizontally as it is in the lachrymal bone (see Fig. 8).

The remaining elements of the infraorbital series each consists of little more than an ossification around the sensory tubule; only the second bone is produced into a shallow flange ventrally. There are apparently only three infraorbital bones in addition to the lachrymal. The second in the series is greatly elongate, and extends along virtually the entire ventral margin of the eye. The third bone is moderately elongate but the fourth is much reduced in size, being in that respect comparable with the sixth bone in the infraorbital series of *Hemichromis* (cf Fig. 8 with fig. 9 in Greenwood, 1985).

It is impossible to tell from the material examined whether or not the second and third bones are compound elements, a possibility suggested by the low total number of bones and the elongation of the second and third elements.

The *supracleithrum* and *posttemporal bones* (Fig. 9) differ from those in *Hemichromis* only in the shorter and wider arms of the posttemporal. For comments on the possible value of these elements as indicators of phyletic relationships see Greenwood (1985: 147) where Van Couvering's (1982) ideas on that point are discussed.

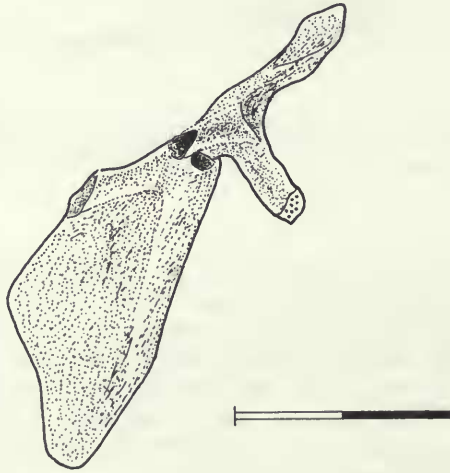


Fig. 9 *Anomalochromis thomasi*. Right supraclathrum and posttemporal.

Pectoral girdle and postcleithra (Figs 10A & B). This complex shows few noteworthy characters, except that the spine on the head of the second postcleithrum is well-developed and is much more obvious than the spine in *Hemichromis*. It was impossible to establish whether or not the spine in *Anomalochromis* is associated with a muscle sheet from the first rib (Greenwood, 1985: 154).

Axial skeleton. As in the majority of African cichlids there is only a single *predorsal bone* (see Oliver, 1984).

Excluding the fused PU_1 and U_1 centra there are 23 (f1), 24 (f35) or 25 (f3) *vertebrae*, of which 12 are abdominal in position, and 11 (f1), 12 (f35) or 13 (f3) are caudal elements. The lectotype and one paralectotype have total vertebral counts (excluding the fused PU_1 and U_1 elements) of 25 (ie 12 + 13), the second paralectotype (39.0 mm SL) has a teratologically distorted vertebral column in which the number of centra cannot be ascertained with certainty, but appears to be 25.

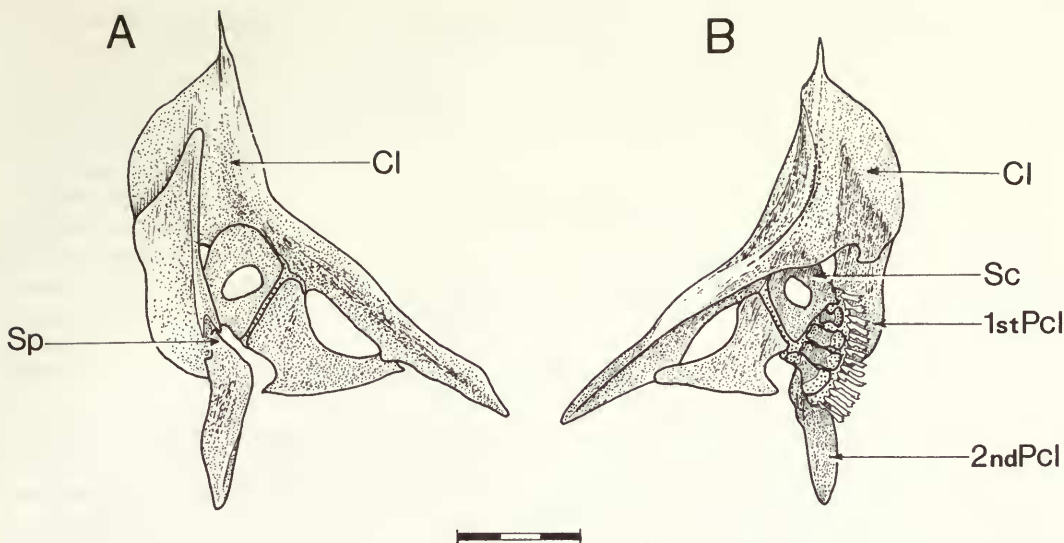


Fig. 10 *Anomalochromis thomasi*. Left pectoral girdle and postcleithra in: A, medial, and B, lateral view. Cl=Cleithrum. 1stPcl=1st Postcleithrum. 2ndPcl=2nd Postcleithrum. Sc=Scapula. Sp=Spine on head of 2nd Postcleithrum.

A low *apophysis* for the insertion of the *retractores arcuum branchialium* muscles is present on the third abdominal vertebrae; the two sides of the apophysis do not meet ventrally.

Epipleural bones are present on all pleural ribs in the two alizarin specimens examined; *epineurals* are present only on the first two vertebrae, which are without pleural ribs.

Caudal fin skeleton. All five hypurals are free in one of the two alizarin specimens examined, but in the other the 3rd and 4th hypurals are either fused or very closely apposed to one another. In both these specimens, and in all those specimens radiographed, the first hypural is noticeably deeper (from twice to 3 times so) than the second hypural. Further information on the condition of the hypurals, in particular the possible extent of the fusion, could not be obtained from the radiographs.

Well-developed dorsal and ventral accessory cartilages are present; both are free from the thin cartilaginous strip lying along the distal margin of the epurals, hypurals and the parhypural. This strip is not continuous across the gap separating the 2nd and 3rd hypurals, and no cartilaginous plate occupies that gap. Ventrally, a second and smaller accessory cartilage lies between the haemal spines of the 2nd and 3rd preural vertebrae; it too is free from the major ventral accessory cartilage, and it is not connected with the strip lying along the distal margins of the 1st and 2nd hypurals and the parhypural.

An unusually prominent 'stegural' plate is developed on the base of the uroneural complex. In one of the alizarin specimens there is a double neural arch and spine on the centrum of the second preural vertebra; in the other specimen there is a single but expansive arch and spine.

The parhypural is apparently without an hypurapophysis, an unusual condition in African cichlids.

Dentition (Figs 11A-C). Teeth situated anteriorly in the outer row of both jaws are of two kinds: relatively slender unicuspid with slightly incurved crowns, or relatively slender teeth with compressed, somewhat obliquely sloping crowns which sometimes have a faint indication of a much smaller minor cusp appearing as a shallow notch in the crown. Laterally and posterolaterally unicuspid in the outer tooth row are noticeably more slender than those occurring anteriorly, and their crowns are but slightly incurved.

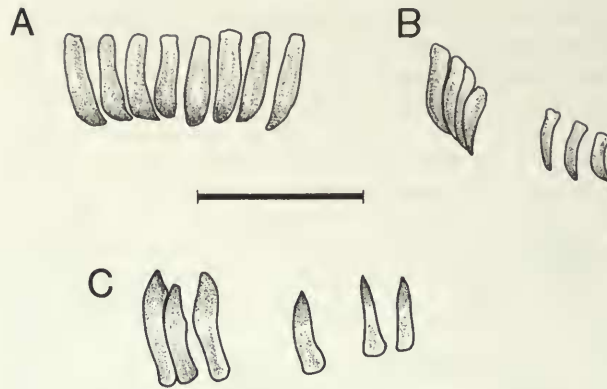


Fig. 11 *Anomalochromis thomasi*. Oral dentition; outer row. A, Anterior premaxillary teeth on either side of the premaxillary symphysis; frontal view of labial aspect. B, Premaxillary teeth from the anterior part and the extreme posterior part of the left premaxilla; labial aspect viewed laterally. C, Teeth from the anterior, middle and extreme posterior part of the left dentary; labial aspects as viewed laterally. All are from a fish ca 40 mm SL. Scale = 1 mm.

The predominant form of tooth situated anteriorly and laterally in the jaws is correlated with the fish's size. Unicuspid anterior teeth are found only in fishes more than 40 mm standard length, and even in specimens as long as 45 mm SL some weakly bicuspid teeth with expanded crowns are often present. Similarly, the proportion of slender unicuspids occurring laterally and posterolaterally increases with size. Only the posterior one or two teeth in the smallest fish examined (25 mm SL) are unicuspids.

All teeth in the inner rows are unicuspid, even in the smallest fish examined. Anteriorly and anterolaterally, the inner teeth of the upper jaw are arranged in from 1 to 3 irregular rows, but generally in 2 rows. There is a single row posteriorly, extending to a point about half-way along the alveolar surface of the premaxilla. The interspace separating the inner rows from the outer series, especially towards the midline of the jaw, is sometimes greatly reduced in size.

Inner tooth arrangement in the lower jaw is like that in the upper jaw, except that the interspace between the inner series and the outer row is more obvious, and the reduction of the inner series to a single row takes place more anteriorly in this jaw. As in the upper jaw, the inner row extends posteriorly only for about half the length of the alveolar surface.

Anatomy

The small adult size of *A. thomasi*, coupled with the generally poor preservation of most specimens in the BMNH collection, have rendered difficult any precise study of soft anatomy. For example, it has proved impossible to determine the pattern of intestinal coiling, a feature probably of some importance in assessing phylogenetic relationships amongst cichlids (see Zihler, 1982); nor was it possible to learn much about other internal organs. Some observations could, however, be made on the cranial musculature and ligaments, and on the muscles of the gill-arches.

The *jaw musculature* is essentially similar to that described for *Hemichromis* (Greenwood, 1985: 155–157), but in *A. thomasi* the tendon A_{1b} of the *adductor mandibulae* 1 muscle, although closely associated with the tendon of *adductor* A_w , remains discrete throughout its passage across the latter tendon before it inserts on the nipple process of the anguloarticular bone. The tendon of *adductor mandibulae* 3, which inserts on Meckel's cartilage, is long, as is that from *adductor mandibulae* 1 to the maxilla; the tendon of *adductor mandibulae* 2, inserting on the poorly defined coronoid process of the dentary, is short and deep.

A small part of the *adductor arcus palatini* muscle inserts on the palatine, a feature apparently characteristic of all African cichlids (see Greenwood, 1985: 156).

The dorsal musculature of the gill-arches is like that in *Hemichromis* and thus is of the generalized cichlid pattern (see Greenwood, 1985: 159–162). As in other species with this type of musculature, only a small slip of the *levator externus* IV muscle passes to the 4th epibranchial, the greater part inserting on the horn of the lower pharyngeal bone.

A detailed study of ventral gill-arch muscles, and the associated ligaments of the gill-arches, could not be made.

Ligaments associated with the jaw and palatoquadrate arch. Unlike *Hemichromis*, *A. thomasi* has a full complement of these ligaments (see Greenwood, 1985: 158–159), including a definite anteroventral palato-maxillary ligament. The broad, vertical lateral ethmoid to palatine ligament (absent in *Hemichromis*) is not subdivided and lies behind the origin of the palatopalatine ligament. The palato-maxillary ligament (also wanting in *Hemichromis*) is broad and well-defined.

That *A. thomasi* has a full complement of ethmo-palatine and palato-maxillary ligaments is probably correlated with the species having, unlike *Hemichromis*, a generalized and double articulation between the ethmoid and palatine bones (see Greenwood, 1985: 158).

Squamation. Except for those scales above the upper lateral-line, and on the thoracic and ventral abdominal regions, all other scales are weakly ctenoid. The circuli are arranged in a pattern essentially of the 'gothic arch' type (Trewavas, 1973: 14), especially towards the centre of the scale. Circuli lying more laterally are often arranged almost in parallel, but converge slightly as they approach the exposed margin of the scale.

There are from 24–26 scales in the lateral-line series, the last in the upper series not overlapping, in the vertical plane, the first scale of the lower series. The beginning and the end of each series respectively is thus separated by one, and generally two vertical scale rows. Scales in the upper lateral-line are separated from the base of the dorsal fin by one large and one much smaller scale over most of the line's course.

Gill-rakers and buccopharynx. Rakers on the epibranchial of the first arch are greatly reduced in size, and number one or two. A single raker occurs in the angle between the epibranchial and ceratobranchial of this arch, and there are 5 or 6 short rakers carried on the ceratobranchial.

Although the roof of the buccal cavity immediately in front of, and slightly medial to the upper pharyngeal bones is somewhat thickened and thrown into a number of deep folds, it cannot be described as forming a prominent prepharyngeal pad such as occurs in *Pelmatochromis* and *Thysia*. It is certainly in no way comparable with the visor-like pad found in *Chromidotilapia* and certain other genera (Trewavas, 1974: 389; Greenwood, 1983: 265).

The relationships of *Anomalochromis thomasi*

In his original description of *Paratilapia thomasi*, Boulenger (1915) suggested that the species '... appears to be closely related to *Paratilapia dorsalis*', but gave no substantiating evidence for his suggestion. *Paratilapia dorsalis* Pellegrin is currently treated as a synonym of *Pelmatochromis nigrofasciatus* (Pellegrin); see Thys van den Audenaerde (1968) and Trewavas (1973).

Boulenger's (1915) suggestion is clearly based on an overall and superficial similarity between the two species. From Trewavas' (1973) revision and redescription of *Pelmatochromis* Steindachner it is clear that *A. thomasi* shares no uniquely synapomorphic features with any members of that genus, and indeed Trewavas excluded it as being '...not a true *Pelmatochromis*'; she did not, however, suggest where its affinities might lie, nor did she comment on Thys van den Audenaerde's (1968) alignment of the species with *Hemichromis*. On the basis of synapomorphies, *A. thomasi* cannot be considered closely related to *Chromidotilapia* or *Pelvicachromis* (pers. obs.), the two genera amongst which Trewavas distributed, either explicitly (Trewavas, 1974) or implicitly, the species which Regan (1922) had included in his concept of *Pelmatochromis*.

Thys van den Audenaerde's (1968) paper referred to above was concerned, essentially, with an attempt to unravel the phylogeny and relationships of the numerous species, including *A.*

thomasi, then placed in *Pelmatochromis*, *sensu* Regan (1922). Although several anatomical features were used in that attempt, the unique nature of the palato-ethmoidal articulation in *Hemichromis* (see Greenwood, 1985) was then unknown, as was the absence of a latero-sensory canal in the anguloarticular of both *A. thomasi* and *Hemichromis*. The discovery of the latter feature would certainly seem to strengthen Thys van den Audenaerde's (1968) idea of a close relationship between the two taxa (see p. 265). Similarities in coloration and breeding biology, characters which also influenced Thys van den Audenaerde's views, are of equivocal value (see below).

In the following year, Thys van den Audenaerde (1969) suggested, without reference to the 1968 paper, that his newly described species *Tilapia joka* was related to *A. thomasi*. *Tilapia joka*, unlike *A. thomasi*, has a fully developed latero-sensory canal in the anguloarticular and, as far as I can determine, shares no synapomorphies uniquely with *A. thomasi*. A close relationship between the two taxa is most unlikely.

It has also been thought that the genus *Thysia* Loisel & Welcomme is related to *A. thomasi*. In their paper describing *Thysia*, Loisel & Welcomme (1972: 53 *et seq*) took up the ideas expressed by Thys van den Audenaerde (1968) and, developing them further, postulated that *Thysia*, together with '... the *Hemichromis bimaculatus*-*Pelmatochromis thomasi* group within *Hemichromis sensu lato*', and the *Hemichromis fasciatus* complex within *Hemichromis*, '... can be considered an oligophyletic assemblage comparable to *Tilapia sensu lato*'. Loisel & Welcomme's ideas are discussed fully in Greenwood (1985: 164-169), and the conclusion reached that, if synapomorphies and not just overall levels of similarity are used to determine relationships, the full Loisel-Welcomme hypothesis could not be substantiated. That part of the hypothesis which indicates an *A. thomasi*-*Hemichromis (sensu lato)* relationship, however, does now seem to be one that can be substantiated.

In my 1985 paper I expressed reservations about using the absence of an anguloarticular sensory canal as a synapomorphy to link *Hemichromis* and *A. thomasi* on the grounds that it was a 'loss character'. Further investigation and reflection (see p. 258) has, however, led me to alter my earlier opinions. I would now argue that the absence of the canal in those taxa alone amongst the cichlids and their outgroup relatives is more parsimoniously treated as a true synapomorphy indicative of recent common ancestry. That conclusion is strengthened by there being no contra-indicative synapomorphies suggesting that either taxon has closer affinities with any other taxon or lineage. The wider-based comparative anatomical investigation which led to my changed viewpoint failed to substantiate Loisel & Welcomme's (1972) proposed relationship of either *Hemichromis* or *A. thomasi* with *Thysia*, neither did it indicate a close relationship of *A. thomasi* with *Chromidotilapia*, *Pelvicachromis* or *Pelmatochromis*.

The only other worker to consider the relationship of *A. thomasi* is Voss (1980), who used for that purpose data obtained from his comparative studies on the ethology and coloration of *A. thomasi* and certain other African cichlids. Voss' work is, unfortunately, limited by the extent of the outgroup comparisons he could make since very few observations as detailed as his are available, even for members of the Cichlidae. As with most of those authors who used morpho-anatomical features to investigate the relationships of *A. thomasi*, Voss' approach is not a cladistic one, but is based on degrees of similarity in characters whose polarity cannot yet be determined.

Voss' (1980) conclusions derived from details of coloration and colour patterns seem rather indecisive and even contradictory. In one place (Voss, 1980: 47) he says that '... On the scheme of colored markings, *P. thomasi* and *H. bimaculatus* appear to us then rather closely related. It is the same with *T. [Thysia] ansorgii*, but in a distinctly lesser way. This species seems nearer *P. thomasi* than *H. bimaculatus* (on this scheme at the very least)'. Elsewhere (*op. cit.*: 87) he comments that '... *H. bimaculatus*, *P. thomasi* and *T. ansorgii* unquestionably show a certain relationship on the basis of their colored markings (especially the first two [species] mentioned). Still, these same species can be set widely apart by these same elements. According to these criteria, it is rather then of a group in which the species are related in a rather loose manner'. In another context (*op. cit.*: 86), the presence of a silvery genito-anal spot, Voss believes that '... there is not much separation' between the *Pelvicachromis*-*Nanochromis*-*Chromidotilapia*

group and the genus *Thysia*; no mention is made here of *A. thomasi*, which lacks the genito-anal spot.

Based on a study of ethological features, Voss (*op. cit.*: 118) notes that '... *P. thomasi*, *H. bimaculatus*, and *Thysia ansorgii* have numerous common points which allow placing them together, but also some important differences in their patterns which lead one to think that they are already very distant'. He concludes that remark with the seemingly contradictory statement... 'Moreover, the ethological data does not justify a classification of *H. bimaculatus* and *P. thomasi* in different genera'.

Obviously a lot more data on ethology and coloration are required before such information is likely to be of value in unravelling phyletic relationships. Those data, too, should be derived from a wide range of cichlid taxa, and from out-group taxa as well.

The previously most recent generic assignment of *A. thomasi*, one based mainly on similarities in ethology and coloration, was to the genus *Hemichromis* (see Wilson & Loiselle, 1980). That placement would, in my opinion, be negated by *A. thomasi* having a plesiomorphic palato-ethmoidal articulation and not the highly derived condition found, uniquely, in *Hemichromis* (Greenwood, 1985); it is also weakened by the equivocal nature of the behavioural and colour similarities on which Wilson & Loiselle place so much emphasis (see above). However, I would certainly subscribe to the idea of *A. thomasi* and *Hemichromis* being sister taxa (see p. 258, and discussion in Greenwood, 1985: 168–169).

On the information currently available it is impossible to relate a *Hemichromis*-*Anomalochromis* lineage to any other African cichlid species or group of species; for that reason I would propose that the lineage be given the informal status, and epithet, of the hemichromine group, but would suggest that it is more readily defined and is phylogenetically more coherent than at least two other informal groups now recognised, namely the tilapiines and the haplochromines.

Some might, and some no doubt will argue, on the basis of Regan's division of cichlids into a *Haplochromis*-group and a *Tilapia*-group, that *A. thomasi* cannot be closely related to *Hemichromis* since it has a *Tilapia*-type neurocranial apophysis whilst all *Hemichromis* species have an apophysis of the *Haplochromis*-type. The validity of this supposedly diphyletic division has been questioned by several workers (see Greenwood, 1978), an uncertainty reinforced by the *Tilapia*-type apophysis being the plesiomorphic condition and thus of no value as an indicator of close relationship amongst those species with this apophyseal type. Furthermore it has yet to be demonstrated that any unifying synapomorphy exists among the very large number of species having an apophysis of the *Haplochromis*-type.

In its ontogeny, the *Haplochromis*-type apophysis first passes through a condition comparable with the adult *Tilapia*-type (Ismail *et al.* 1982). Thus it is possible that the occurrence of *Tilapia*-type apophyses in species otherwise apparently related to taxa with a *Haplochromis*-type, could be interpreted as demonstrating paedomorphosis in this character. Such an explanation might well apply to *A. thomasi*, a species whose members reach only a small size at sexual maturity, and one apparently exhibiting, in the adult, a paedomorphic juxtaposition of certain bones in the ethmoverine complex of the neurocranium (see p. 261).

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